EGGSHELL SITES FROM THE CRETACEOUS-TERTIARY TRANSITION IN SOUTH-CENTRAL PYRENEES (SPAIN).

Nieves LÓPEZ-MARTÍNEZ

Dpto. Paleontología, Facultad de Geología, Universidad Complutense de Madrid (Spain)

ABSTRACT

Near one hundred fossil sites containing dinosaur and avian eggs and eggshells have been recorded from coastal and non-marine deposits of late Cretaceous to late Paleocene age in South-central Pyrenees. Five eggsite types have been distinguished, three of them with autochthonous and two with allochthonous assemblages. The egg-bearing sediments consist in marine sandstones from the Aren Formation, and coastal and non-marine red beds from the Tremp Formation. Inferred nesting paleoenvironments range from sand beaches and strand plain at the seashore (Aren Sandstone sites), to tidal mud flats in lagoonal margins (La Posa Grey Marls, lower Member of the Tremp Formation), and perilagoonal, estuarine and alluvial flood plains (bioturbated siltstones, variegated claystones, sandstones and conglomerates of the Tremp red beds). About thirty ootaxa, mainly from tubospherulitic, prismatic and ratite morphotypes have been observed, which greatly overpass the dinosaur and avian diversity deduced from bones. These sites indicate a nest-fidelity reproductive behaviour for Pyrenean dinosaurs and birds. A decrease in abundance and diversity is recorded from late Campanian to Maastrichtian times, while a recovery occurs in late Paleocene.

INTRODUCTION

The South-central Pyrenees (Northern Spain) contain a rich geological record with excellent outcrops documenting the mass extinction around the Cretaceous-Tertiary boundary. Basinal, shallow-marine and non-marine deposits several thousands meters thick can be laterally followed for hundreds of kilometres (figures 1 and 2). Their fossil content allows to establish a well-constrained chronology through different biostratigraphic scales, calibrated by magnetostratigrphy and isotopic content (Ardèvol *et al.*, 2000; Galbrun *et al.*, 1993; López-Martínez *et al.*, 1998). The coastal deposits in this region contain a rich fossil record of dinosaurs and other vertebrates from the Cretaceous-Tertiary transition, specially relevant for unravelling the pattern of their evolutionary crisis.

During mid-twenty century, fossil sites with dinosaur bones, eggs and footprints were discovered in the Tremp basin (Talens, 1955; Lapparent & Aguirre, 1956; Lapparent, 1959). Palaeontologists focused mainly in the description of dinosaur bones and footprints (Llompart, 1979; Llompart & Krauss, 1982; Llompart *et al.*, 1984; Brinkmann, 1984; Casanovas *et al.*, 1987, 1993, 1999a, b). Although dinosaur eggs and eggshells, intensively vandalised by dealers for a long time, are much more abundant than bones or tracksites in

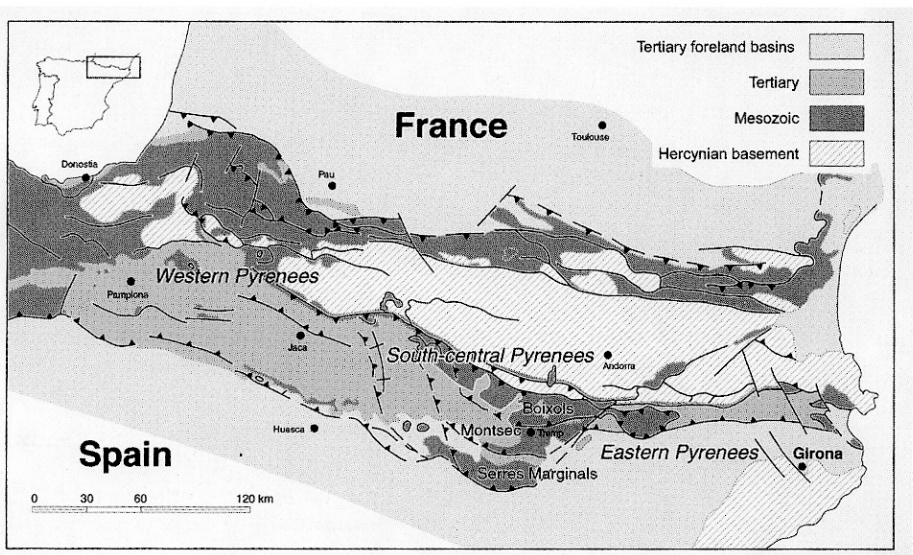


Figure 1. Geological map of the Pyrenees, indicating the tectonic units of the South-central Pyrenees (from E. Vicens). Details of the Boixols and Montsec area is shown in the map figure 2.

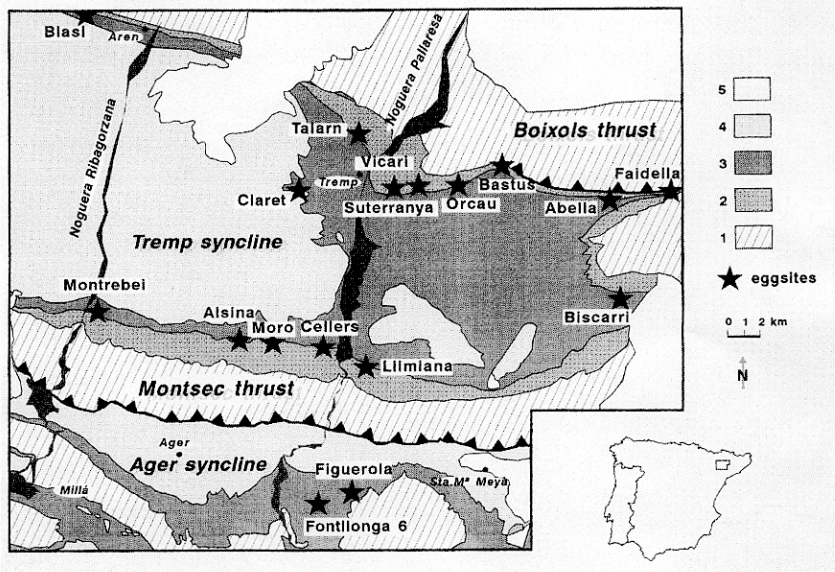


Figure 2. Geological map of the Tremp and Ager synclines (South-central Pyrenees, Lleida), with some of the main egg and eggshell fossil sites. 1, Upper Cretaceous and older; 2, Aren Sandstone; 3, Tremp Formation; 4, Ilerdian; 5, Upper Eocene and younger. From Losantos *et al.*, Institut Cartogràfic de Catalunya.

Southern Pyrenees, only recently some of these sites and fossil eggs have been studied and published (Kohring, 1989; Moratalla, 1993; Sanz *et al.*, 1995; Vianey-Liaud & López-Martínez, 1997). Thanks to modern sedimentological, taphonomical and microscopical techniques, fossil eggs and eggsites become relevant for palaeobiology and biochronology, documenting dinosaur distribution, diversity, reproductive behaviour, habitat and extinction. They are also appreciated by an increasing social interest about the dinosaur fossil record.

From Late Cretaceous to Late Paleocene, around one hundred eggsites have been found in South-central Pyrenean, bearing a high eggshell diversity for a relatively small area. Some of them are unique in the world because of their palaeogeographical situation along ancient sea shores. The discovery, interpretation and dating of many of these sites are the results of a team work carried on during the last eight years in the frame of three research projects on the Cretaceous-Tertiary transition in Southern Pyrenees. We present here a summary of the South-central Pyrenean eggsites, their features and content in their chronostratigraphic and sedimentary context.

GEOLOGICAL SETTING

The South-central Pyrenees form a part of the Pyrenean orogen dominated by southward vergent structures between the Nogueras thrust at the north, the frontal thrust of the Sierras Marginals at the south, the river Segre valley at the east and the Cinca at the west (figure 1).

In the transition from late Cretaceous to early Tertiary times (late Campanian-late Paleocene, about 80-55 million years ago), the Pyrenean basin became completely filled up with regressive coastal and non-marine deposits. Overlying the deep oceanic facies dated around late Santonian-middle Campanian, slope and shelfal clastic deposits prograded north and westwards, filling finally up the foredeep basin with continental red beds. This synorogenic deposition occurred while successive anticlines grew progressively from east to west, due to the oblique collision between the Iberian and European continental plates. As the collision continued, the Pyrenean basin deposits became subsequently fragmented into several tectonic units. One of them is the Central South-Pyrenean Unit (Séguret, 1972), where most of the eggsites studied here are located. From north to south, this unit contains the Boixols, Montsec and Serres Marginals thrust sheets. These sheets moved southwards in a sequence of piggy-back thusts, subsequently affected by out-of-sequence thrusts and backtrusts. The sedimentary thickness of these three units thin out southwards.

The Boixols thrust sheet constitutes the northern boundary of the Tremp basin, between the Boixols-Sant Corneli-Turbón anticlines in the north and the Montsec thrust at the south (figures 1 and 2). The Boixols front thrust active area was situated offshore at the platform-slope boundary; it preserves the first signs of the Pyrenean basin emergence during late Cretaceous, and the oldest record of dinosaurs in the South-central Pyrenees (Plaziat, 1972). The Montsec thrust sheet consists of a large, east-west oriented synclinorium which supports the Tremp basin. This basin opens westwards during the Paleogene, and its proximal deposits (the Tremp-Graus basin s.s.) have been thrusted over the distal ones (the Jaca-Pamplona basin). South of the Montsec thrust, the Serres Marginals thrust sheet (including the Ager syncline) is a mosaic of tectonic scales decreasing in size southward and eastward, made up by adjacent synclinals floating over Triassic evaporites. They represent the fragmented deposits of the southern passive margin of the Pyrenean basin, while the position of the northern margin is not well known.

The eggshell sites studied here are placed in three main areas: 1) the Tremp syncline with its northern and southern flanks, in the Montsec thrust sheet; 2) the Ager syncline in the Sierras Marginals thrust

sheet, with a southern flank only because its northern flank disappeared below the Montsec thrust, and 3) the Coll de Nargó syncline, located east of the Tremp basin in the Montsec thrust sheet (figure 1). We have included for comparison an eggsite from the Sierras Exteriores Aragonesas, in the southern flank of the Jaca-Pamplona synclinorium (La Peña, Table I). Other eggsites from the South-eastern Pyrenees (Pedraforca thrust sheets) will not be studied here.

In the studied areas, three lithostratigraphic formations can be recognized for the Cretaceous-Tertiary transition, from bottom to top:

- Les Serres Limestone (shallow marine calcarenites about 2000 m thick, Souquet, 1967);
- Aren Sandstone (marine mixed arenites up to 3000 m thick) and
- Tremp Formation (coastal and non-marine red beds up to 900 m thick, Mey *et al.*, 1968).

Up to now, the dinosaur fossil eggs have been only found in the two latter Formations. A geological map is shown in figures 1 and 2; field views, stratigraphical sections and chronology are shown in figures 3 to 7.

Les Serres Limestone appears mainly in southern and eastern areas of the South-central Pyrenees (e.g. Serres Marginals). This formation consists of either massive, bedded or cross-stratified shelfal limestone bodies occasionally rich in rudist fossils. In its upper part, local intercalations of quartz sandstones mark a transition with the Aren Sandstone (figure 5).

The Aren Sandstone is particularly developed in the Tremp basin and Coll de Nargó syncline. It forms a huge clastic wedge at the shelf-slope boundary, made up by mixed, bioclastic and terrigenous fine-grained to microconglomeratic sandstones with well-rounded quartz grains, frequently showing large-scale cross stratification (figure 3). Deposits of similar lithology represent different depositional environments, e.g. turbidites, shelfal channels, coastal barrier islands and tidal estuarine bodies (Nagtegaal *et al.*, 1983; Díaz Molina, 1987; Ardèvol *et al.*, 2000).

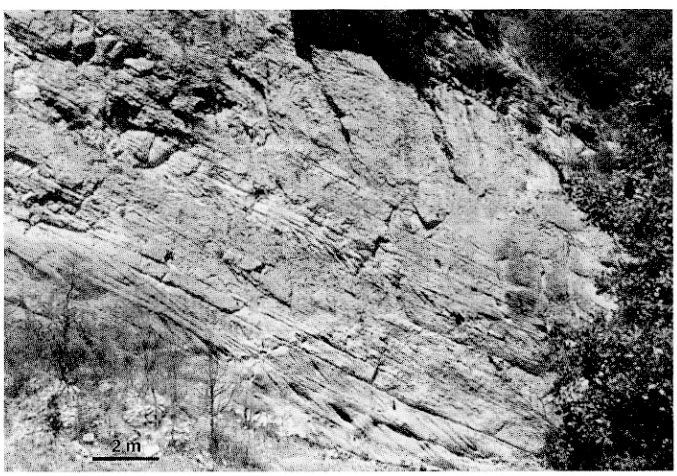


Figure 3. Field view of large-scale, sygmoidal cross-stratification indicative of tidal currents in the Early Maastrichtian Aren Sandstone, Noguera Ribagorzana section (Huesca, Spain).

The Tremp Formation extends over most of the South-central Pyrenees and adjacent regions, indicating the complete infilling and emergence of most of the Pyrenean basin. Its red beds consist mainly in variegated marls and clays rich in paleosols, peritidal limestones, grey marls and coal, as well as fluvial sandstones and conglomerates. Units 1 to 4 have been defined according to their carbonatic (Units 1 and 3) or clastic (Units 2 and 4) dominant lithology. The Cretaceous-Tertiary boundary is situated near the top of Unit 2 (figures 4 and 5; López-Martínez *et al.*, 1998).

The precise relations between these formations are complex and their chronology is controversial.

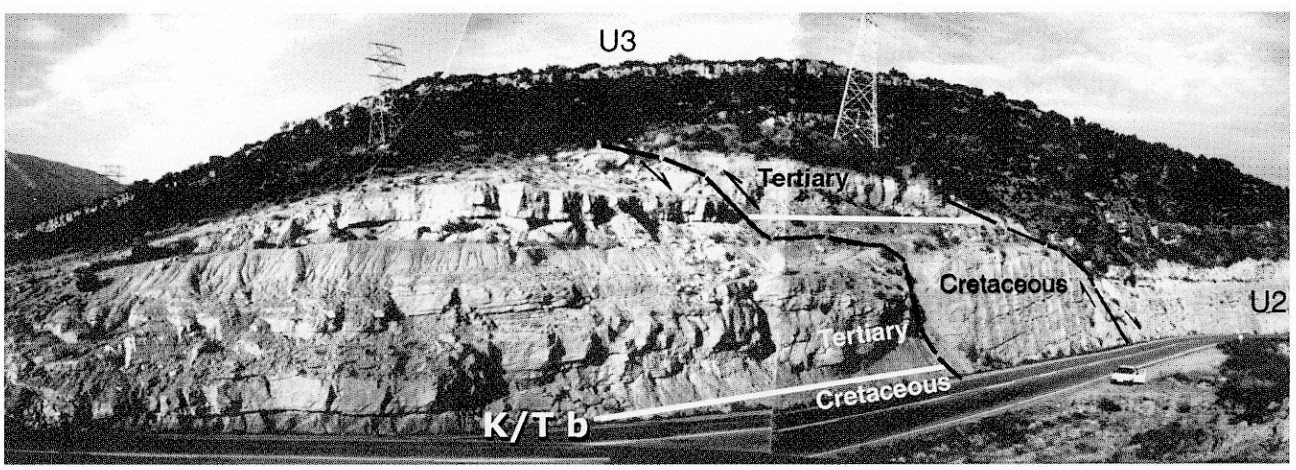


Figure 4. Field view of Tremp Formation red beds in the Ager syncline, Fontllonga section, showing the transition from clastic-dominated Unit 2 ("Reptile Sandstone") to carbonate-dominated Unit 3 ("Vallcebre Limestone"). The position of the Cretaceous/Tertiary boundary is indicated (white line), within a 3-m thick reddish clay interval near the top of the "Reptile sandstones". Faults are signalled by black dashed lines.

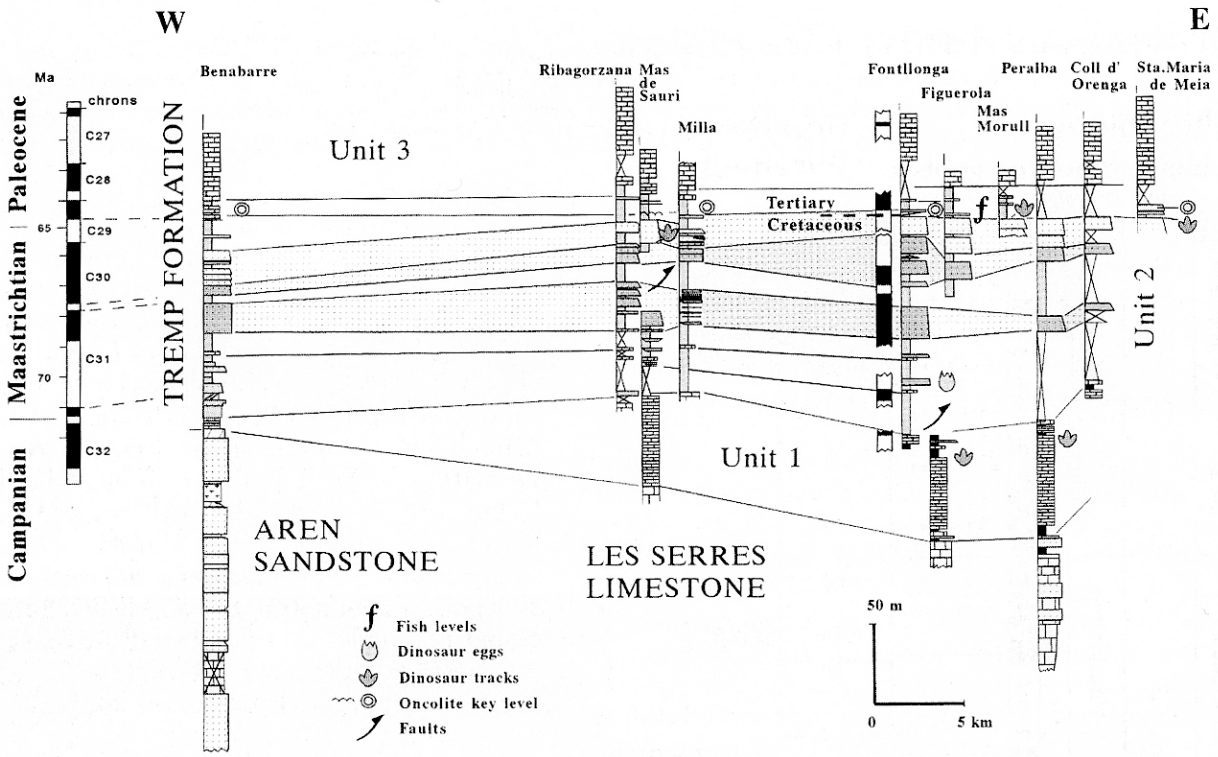


Figure 5. Stratigraphic correlations between Les Serres Limestone, Aren Sandstone and Tremp Formation in the Ager syncline and Benabarre area (from López-Martínez *et al.*, 1998). Dinosaur tracksites and the eggsite Fontllonga-6 are indicated, as well as Paleocene fish sites and a large key oncolith level. Magnetostratigraphic correlation is based on Galbrun *et al.* (1993).

They are roughly superposed, though a more detailed geometry shows lateral transitions between them. The upper part of Les Serres Limestone is laterally equivalent to the Aren Sandstone (figure 5; see López-Martínez *et al.*, 1998; Vicens *et al.*, 1999). The Aren Sst. wedges out south and eastwards, which puts in contact Les Serres and Tremp Formations (Garrido Megías & Ríos Aragües, 1972, their Figure 20). Moreover, the Aren Sandstone grades eastwards to the lower part of the Tremp Formation (Díaz Molina, 1987; Krauss, 1990; Ardèvol *et al.*, 2000; figure 6). The upper part of Unit 2 of the Tremp Formation containing the Cretaceous-Tertiary boundary interval (figures 4 and 5) does not pass to the Aren Formation but overlies it. Finally, the Aren Sandstone grades north and westward to deep-water clastic deposits (figure 6; Díaz Molina, 1987; Ardèvol *et al.*, 2000; López-Martínez *et al.*, *in press*; Vicens *et al.*, *in press*).

The Tremp syncline deposits have been divided into four depositional sequences, named Aren-1 to Aren-4 (Ardèvol *et al.*, 2000; figure 6). The large majority of the eggsites belong to the Aren-2 sequence (24 localities, containing most of the richest sites; figure 7 and Table 1). Only two localities are situated in Aren-1 sequence, three localities in Aren-3 and one in Aren-4. The dating of these sequences has been possible by means of planktic foraminifera (data from X. Orue-Etxebarria) in the oceanic deposits, correlated with

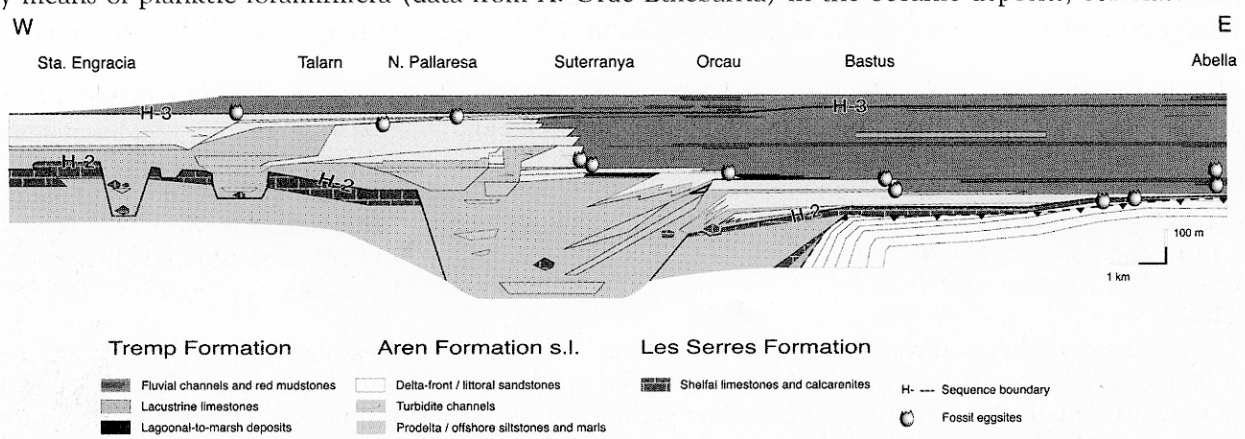


Figure 6. Cross-section along the northern flank of the Tremp syncline (see localities in figure 2), showing the transition between different sedimentary facies of Aren Sandstone s.l. (including slope marls) and the non-marine deposits of the lower Tremp Formation; shelfal calcarenites similar to Les Serres Limestone are also present. These deposits pass further westward to basinal deposits. Sequence boundaries H-2 and H-3 separate the depositional sequences Aren-1 to Aren-3. (Modified from Ardèvol *et al.* (2000, Figure 11). Egg-bearing localities, from left to right: Talarn, Compuertas, Vilamitjana, Suterranya, Orcau, Bastus, Cal Borrell, Cal Serret and Abella. See chronostratigraphy in figure 7

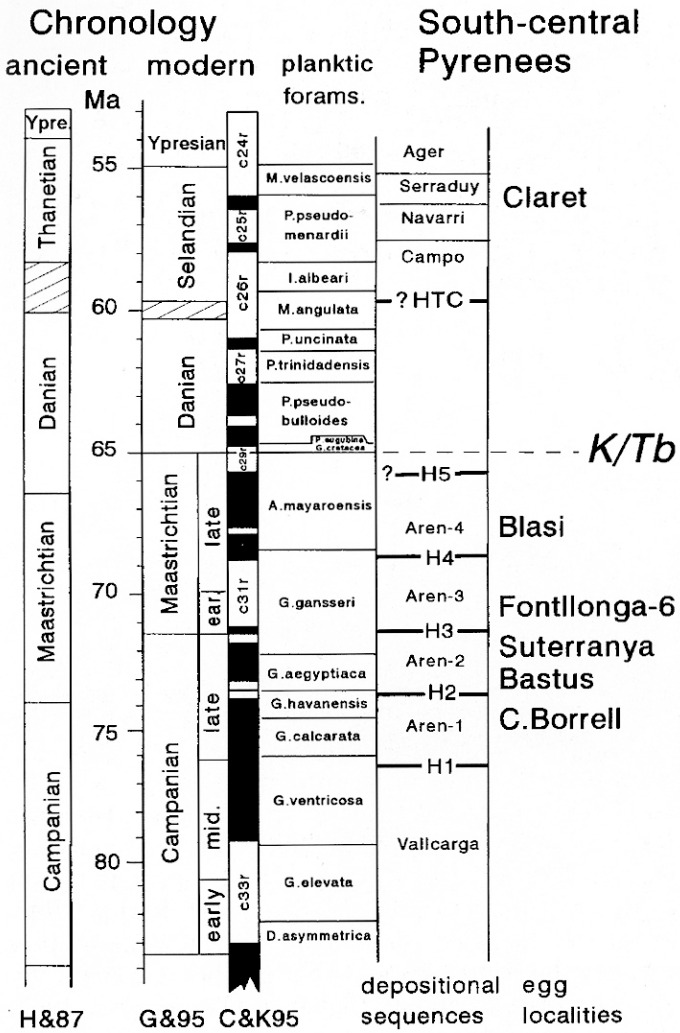


Figure 7. Timescale for the Cretaceous-Tertiary transition: left, old chronostratigraphy (H&87: Haq *et al.*, 1987); centre, new chronostratigraphy (G&95: Gradstein *et al.*, 1995); palaeomagnetic scale, from Cande & Kent, 1995 (C&K95); right, chronological situation of the depositional sequences in South-central Pyrenees (Ardèvol *et al.*, 2000; Luterbacher *et al.*, 1991) and some of the eggsites (see Table I).

the neritic and the non-marine ones by high-resolution stratigraphic analysis (Ardèvol *et al.*, 2000; Vicens *et al.*, 1999; López-Martínez *et al.*, *in press*; figure 7). Some continental sections have been calibrated by biostratigraphic studies and paleomagnetic correlations (Galbrun *et al.*, 1993; figure 4). The lithological formations show to be highly diachronous (figure 6). After compilation of chronological data, the Aren Formation deposits ranges from Middle Campanian to Upper Maastrichtian and the Tremp Formation ranges from Upper Campanian to Upper Paleocene, following the new position of the Campanian/Maastrichtian boundary (Gradstein *et al.*, 1995; figure 7). The chronostratigraphic situation of some egg localities is shown in figures 5 to 7 and Table I.

PREVIOUS STUDIES

The dinosaur eggsites of the Southern Pyrenees were signalled for the first time by Lapparent (1958, 1959), Souquet (1967) and Rosell (1967), particularly in the red beds of the Tremp Formation.

One sample from the Barranc de la Munya (Isona) was studied by Erben *et al.* (1979) in their analysis of some French and Spanish dinosaur eggshells. No description of the site was provided, probably the same site signalled by Rosell (1967, p. 130) on variegated marls from the "Garumnian" (= Tremp Formation). The eggshell study was oriented to support the hypothesis of a gradual dinosaur extinction caused by an increase of abnormal eggs with pathological features at the end of the Cretaceous. Afterwards, eggshells from Coll de Nargó were used to support the hypothesis of dinosaur survival in the Tertiary (Ashraf & Erben, 1986). Both hypothesis however have been rejected by further data about eggshell structure (Vianey-Liaud *et al.*, 1994) and age of the sites (Westphal & Durand, 1990; Galbrun, 1997; López-Martínez *et al.*, 1999b; Vicens *et al.*, 1999).

In his PhD thesis, Moratalla (1993) studied some Spanish fossil eggshells, including material from the Tremp basin. He used the parataxonomical procedure inaugurated by Zhao (1975) for naming eggshell types (ootaxa: oofamilies, oogenera, oospecies), also commonly employed in paleoichnology and palynology when assigning an element to its taxon is not possible. Many authors consider fossil eggs as trace fossils (indirect remains of animal activity), but eggs can instead be considered as anatomical elements of the mother organism and functional embryological organs. Eggshells are produced under strong genetic and physiological controls, and contain phylogenetic information like other structures of the clade Amniota (Board, 1982; Mikhailov *et al.*, 1996; Grellet-Tinner, 1999).

Kohring (1989) and Moratalla (1990, 1991 and 1993; see also Moratalla & Powell, 1994) studied eggs and eggshells from Bastus, one of the most noteworthy dinosaur sites of the southern Pyrenees. These eggs were attributed to hadrosaurs by the former author and to titanosaur dinosaurs by the second author, although no arguments were provided for any of these opposite assessments.

The entire dinosaurs egg record of the world was considered as non-marine until Sanz *et al.* (1995) interpreted the Bastus egg site as a marine sand beach used as nesting grounds for dinosaurs. These authors

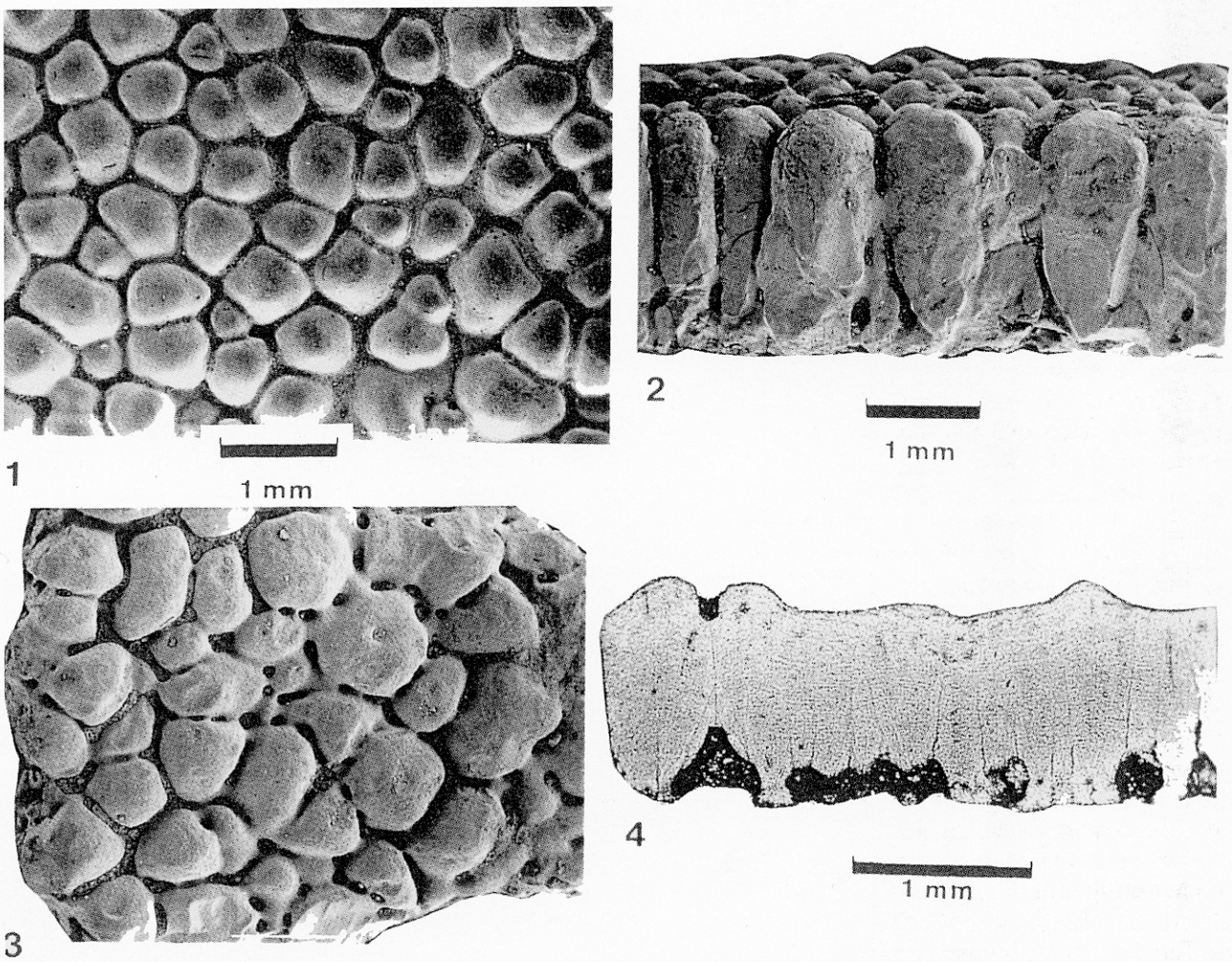


Figure 8. Microscope view of eggshell surfaces and sections of the Megaloolithidae oospecies *Megaloolithus siruguei* from Biscarri (1, 2) and M. *pseudomamillare* from Suterranya (3, 4). (After Vianey-Liaud & López-Martínez, 1997, Figure 11).

documented eggs and eggshell fragments from about three hundred thousand eggs buried on top of Late Cretaceous marine Aren Sandstone. The sedimentology, petrology and palaeontological content of the sandstones surrounding the eggs and eggshells at Bastus indicated that they were buried in freshly emerged marine sands, covered subsequently by a soil. A close proximity between clutches, heavy trampling of the ancient ones, and intensive occupation of the site suggest a nesting-fidelity behaviour of dinosaurs which used to bury their eggs in the same beach for years, similarly to recent marine turtles.

This interpretation was challenged by Sander *et al.* (1998), which consider Bastus as an inland eggsite on the basis of the red colour of the sandstone, the presence of pulmonate gastropods (*Lychnus*) and the comparison with other egg sites from Coll de Nargó in the Tremp Formation, which in fact belong to an entirely different sedimentary context. A further description and discussion on these eggsites will follow below (see also Sanz & Moratalla, 1997 and Ardèvol *et al.*, 1999).

In the Ager syncline, about 20 km. south of Tremp, the most diverse eggshell assemblage of the European fossil record was described by Vianey-Liaud & López-Martínez (1997) at Fontllonga-6 in the Tremp Formation, dated as Early Maastrichtian by palaeomagnetic and biostratigraphic correlations (figure 5). This rich eggshell assemblage forms part of a concentration of vertebrate remains with charophyte oogonia and small oncoliths, probably produced by hydraulic transport. The external features and microstructure of the eggshell fragments lead to the description of seven oospecies from four dinosaur and avian eggshell morphotypes:

- dinosauroid tubospherulitic morphotype, represented by the oospecies *Megaloolithus petralta* and cf. M. *aureliensis*;
- dinosauroid prismatic type represented by three oospecies of Prismatoolithidae (*Prismatoolithus tenuis*, *P. matellensis* and a new oogenus)

Table I. List and dating of the main dinosaur and avian egg-bearing localities from South-central Pyrenees. Each locality may contain several fossiliferous sites; roman letters indicate localities from Aren Sandstone, boldface letters, from Tremp Formation. Numbers in brackets refer to eggsite types: 1, high-occupation eggsite; 2, recurrent nesting area; 3, isolated clutch; 4, mixed eggsite; 5, sparse eggsite.

	West Tremp basin	East Tremp syncline	Ager syncline	Coll de Nargó syncline
Upper Paleocene		**Claret** (4)		
		Tendruy (5)		
Upper Maastrichtian	**Blasi** (4)			
Lower Maastrichtian	**Montrebei** (4)		**Fontllonga** (4)	
Uppermost Campanian	**La Peña** (3)	**Sant Romà** (5)		**Graells** (2)
		Talarn (5)		**Sta. Eulària** (2, 3)
		Compuertas (1)		**Coll de Nargó** (2, 3, 5)
		Vilamitjana		**Sellent** (1, 2, 3, 5)
		Els Nerets (4)		Sellent P (5)
		Llabusta (2)		
		Vicari (5)		
		Suterranya (1)		
		Alsina (5)		
		Biscarri (3, 5)		
		Bco. la Munya (3 ?)		
		Orcau (1, 4)		
		Moro (5)		
		Llimiana (1)		
		Montsec (1)		
		Cellers (1)		
		Roca Regina (1)		
		Bastus (1, 3)		
		Abella (2, 5)		
		Faidella (2)		
Upper Campanian		**Cal Serret** (3)		
		Cal Borrell (1, 3)		

- a new structural type (*Pseudogeckoolithus nodosus*); and
- an ornithoid ratite type, documented by the new ootaxon *Ageroolithus fontllongensis*.

In the same work, four more ootaxa similar to those described from the Aix en-Provence basin were recognized in four additional eggsites from the Tremp basin: *Megaloolithus petralta* and *Ageroolithus fontllongensis* in Moro, *Megaloolithus siruguei* in Biscarri (figures 8 and 19), M. *mamillare* in Bastus (figure 16) and M. *pseudomamillare* in Suterranya (figures 8 and 16). On the base of the eggshell content, a biostratigraphical correlation between the Pyrenean and Aix successions was proposed. According to that, the northern sites (Bastus and Suterranya) would be the youngest ones. Nevertheless the correlation based on eggshells was not coincident with those based on palaeomagnetic successions, which themselves were not congruent to each other. An independent, accurate dating of these non-marine successions remained as a major issue for documenting the dinosaur extinction in Europe.

More recent works on dinosaur eggs and eggshells from the Pyrenees were presented in 1999 at the First international Symposium on Dinosaur eggs and babies (Isona) and López-Martínez *et al.* (2000). Some of these results will be commented below.

EGGSITE TYPES

Up to now, more than thirty localities with near one hundred rich dinosaur and avian egg and eggshell sites have been documented in the Aren and Tremp Formations in the South-central Pyrenees (Table I), from an outcrop area of approximately 1,500 km^2. The deposits containing eggs and eggshells range from marls and siltstones, to sandstones and conglomerates. Preservation of the eggs ranges from entire, tridimensional clutches to small, scattered eggshell fragments. Fossil eggshell assemblages range from monospecific to diverse, reaching up to ten eggshell types in a sample. According to these taphonomic features, five main fossil eggsite types can be distinguished:

- eggsite type 1 (high-occupation eggsite), containing abundant clutches, entire eggs and dense concentrations of eggshell fragments from one or few ootaxa, in a single layer together with bones (e.g. Llabusta, see figure 9; Suterranya, figure 10; Bastus, Sanz *et al.*, 1995, see figures 11 to 13);
- eggsite type 2 (recurrent nesting area), containing several superposed levels with scattered clutches from one or few ootaxa (e.g. Coll de Nargó, Ashraf & Erben, 1986; Sander *et al.*, 1998; Abella, figure 6; Faidella, Bravo *et al.*, 1999, figure 20);
- eggsite type 3 (isolated clutch), containing an isolated, local concentration of eggs and eggshells from an

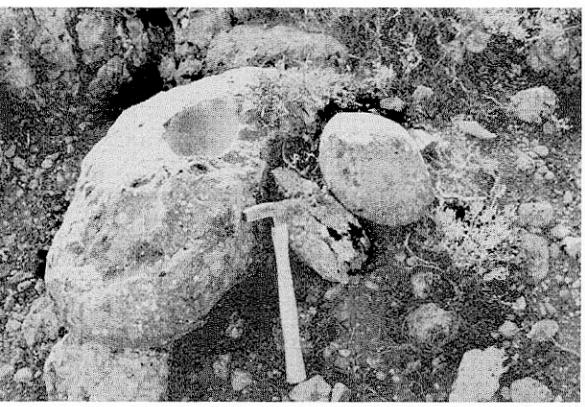


Figure 9. Field view of dinosaur eggs preserved in the Aren Sandstone at Llabusta (Vilamitjana), Uppermost Campanian, Tremp basin (Lleida, Spain).

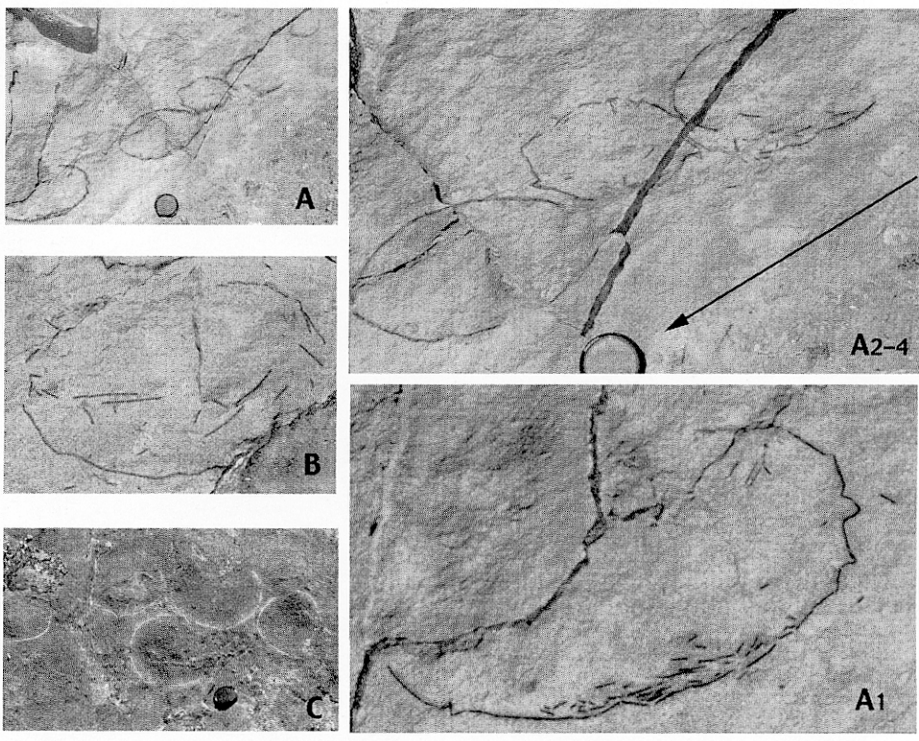
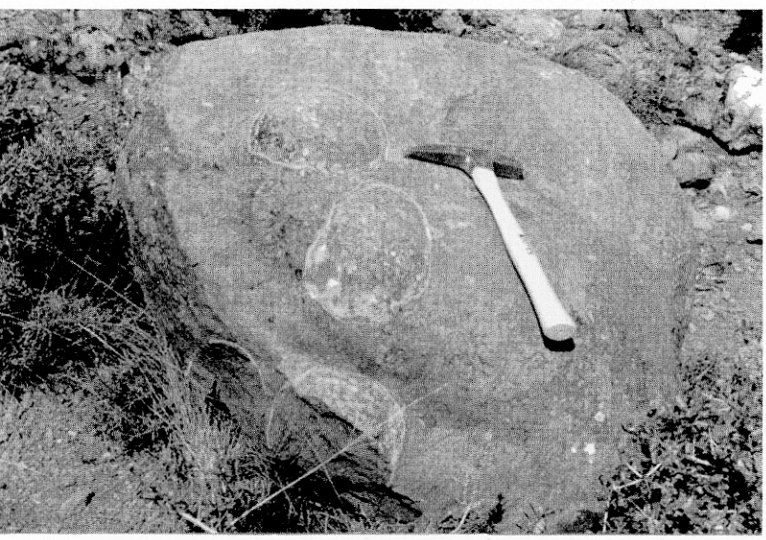
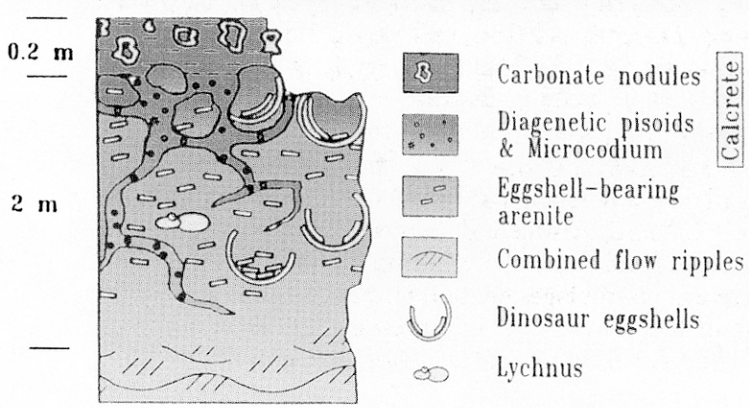


Figure 10. Suterranya dinosaur eggsites in the Aren Sandstone, Uppermost Campanian, Tremp basin (Lleida, Spain); A) A clutch with five eggs in a row is observed in vertical section at Suterranya-3; details are shown at the right: A2-4, eggs 2 to 4; A1, egg 1. The arrow points to dip direction. Eggshell fragments inside eggs 1 and 4 indicate these eggs were hatched and not disturbed from their original position buried in the sand. B) Isolated egg, with large eggshell fragments inside, filled by sand, from Suterranya-3; oblique section view from above. C) horizontal section of a clutch with six eggs arranged in two rows, from Suterranya-1.

Figure 11. Four dinosaur eggs from a single clutch in an *ex-situ* block preserved in the Aren Sandstone at Bastus-1 (Lleida), and scheme of the processes affecting the egg-bearing rock: the marine sandstones with wave ripples pass vertically and laterally to massive "cascarenite" rich in eggs, eggshell fragments and land snails (*Lychnus* and bulimids); incipient beachrock type cement appears before brecciation and subsequent pedogenesis with *Microcodium* colonies, diagenetic pisoids and carbonate nodules (from Díaz Molina, in Sanz *et al.*, 1995).





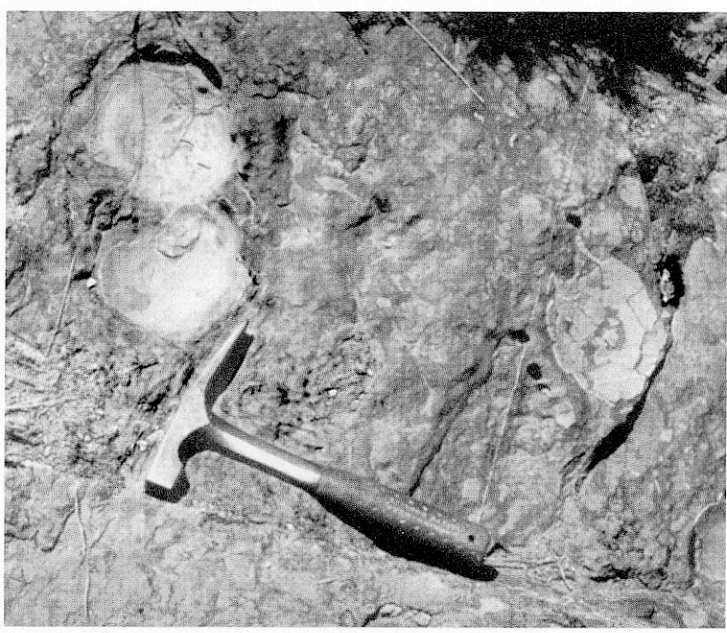


Figure 12. Four dinosaur eggs from a single clutch in the Late Campanian Aren Sandstone at Bastus-2, northern flank of the Tremp basin (Lleida, Spain); white eggs and eggshell fragments are included in reddish host-rock sandstone ("*cascarenite*").

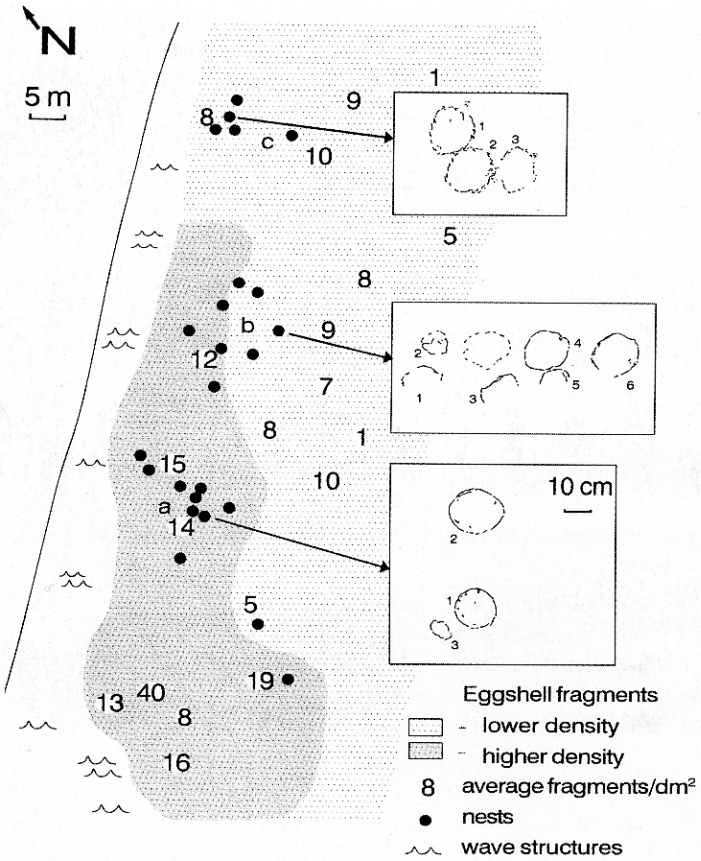


Figure 13. Map of Bastus-1 eggsite, showing the distribution of the main clutches and eggshell fragment density in the massive, reddened sandstones, and the lateral transition towards the northwest to grey sandstone with wave structures. From Sanz *et al.* (1995).

ootaxon, likely from a single clutch (e.g., Sellent, Plaziat, 1972; Biscarri, López-Martínez *et al.*, 2000, see figure 18);

- eggsite type 4 (mixed eggsite), containing a rich assemblage of diverse eggshell fragments from several ootaxa (five or more), usually with bones and mollusc shells (e.g., Fontllonga-6, Vianey-Liaud & López-Martínez, 1997; Blasi-2, López-Martínez *et al.*, 1999a), and

- eggsite type 5 (sparse eggsite), containing only isolated, scattered eggshell fragments from one or few ootaxa, rarely with other fossils (snails, plant debris, etc.).

The first three eggsite types contain autochthonous clutches and eggs, while the fourth and fifth types represent probably allochthonous eggshell assemblages. The autochthonous sites have special interest in palaeobiological studies, since they preserve the original structure of clutches and eggs and their relation with the nesting habitat, allowing to infer the style of reproductive behaviour. All sites are however useful to study the spatial and temporal distribution of dinosaur and avian diversity, and for correlating with other eggshell successions in different regions of the world.

EGGSITES IN THE AREN SANDSTONE

Three out of the seven published localities from South-central Pyrenees are located in Aren Sandstone: Bastus, Suterranya and Moro (Vianey-Liaud & López-Martínez, 1997). In addition to these, twelve new eggshell localities have been located in this marine formation along both flanks of Tremp and Coll de Nargó synclines (figures 2 and 6, Table I). Most of them are situated at or near the top of successive, westwards prograding parasequences of the Aren Sandstone, close to the overlying deposits of the Tremp Formation (Sanz *et al.*, 1995; Ardèvol *et al.*, 1995, 1999; see figure 6).

The egg-bearing beds of Aren Sandstone are homogeneous, fine-grained, compact sandstones cemented with calcite. They are usually massive, although bioturbation can occasionally be observed. Tractive sedimentary structures are absent, but wave ripples and oblique or sygmoidal large-scale cross-stratification are sometimes preserved in underlying and laterally equivalent sandstone levels (figures 3, 11 and 13). The colour of the matrix is generally clear greyish or yellowish, and the eggshells darker (Sellent, Orcau, Suterranya) or lighter (Llimiana, Cellers, Moro, etc.). The main sandstone components are marine bioclasts, such as foraminifera skeletons, fragments of mollusc shells, bryozoa and coralline algae, and well-rounded quartz grains (figure 14). Occasionally, the egg-bearing sandstone bodies are intercalated within sandstone beds bearing marine macrofossils such as rudists and inoceramids (e.g. Bastus and Moro). The marine origin of the Aren Sandstone eggsites is indicated by the composition and fabric of the rock, fossil content and facies analysis (see Díaz Molina, 1987 for Suterranya; Sanz *et al.*, 1995 for Bastus).

The majority of the egg-bearing localities from the Aren Sandstone belong to type 1 (high-occupation) eggsites, such as Cal Borrell-1, Cellers, Llabusta, Suterranya, Bastus-1 to 2 (see figures 9 to 13), etc. Occasionally, other eggsites types are also found in similar situation, such as type 4 mixed with bones in Els Nerets, and type 5 with sparse eggshells in Cal Borrell-2, Moro, Alsina and Talarn. Type 2 eggsites in the Aren Sandstone have been found at Roca Regina (Montsec) and Bastus (sites Bastus-1 to 5). In some of the richest sites, taphonomic evidences indicate that these egg assemblages are autochthonous: aligned eggs in the clutches; near complete eggs, and eggshell fragments fallen inside the egg, presumably during hatching (figures 10 and 15). These sites are thus the original dinosaur nesting places, which preserve most of the

original arrangements and positions of the eggs. The agent of concentration thus was not the transport, but the intensive use of the site for nesting dinosaurs.

The eggshell-bearing sandstones can reach in some of these sites an unusually high content of eggshell fragments (figure 13). This feature characterize this rock-type informally named "*cascarenite*" (from the Spanish "*cáscara*"= eggshell). The origin of this huge concentration of eggshell fragments in the host rock is attributed to trampling of the eggs by hatchlings and by nesting dinosaurs digging new holes, removing and destroying the old clutches. The preserved clutches show rarely seven eggs, more frequently three or four. When is possible to observe several clutches preserved in the same bed (e.g. Cal Borrell-1, Bastus-1-2), they are often too close from each other to allow large sauropods to nest at the same time, side by side (figure 13). This supports the inference of a nesting behaviour similar to the sea turtles: the mothers independently to each other lay the eggs in holes, then abandon the buried nests and leave the beach.

Grades of weathering

The eggsites of the Aren Sandstone can be ordered according to the duration of the emergence of the marine sands, indicated by the intensity of the signs of subaerial weathering. Some sites were rapidly covered by water and by new sediments, while others were exposed for long time. Three grades have been distinguished:

a) no signs of emergence other than eggs. In many cases, the greyish-yellow, marine sandstone bodies containing eggshells are similar to other bodies of the Aren Sandstone without signs of emergence. However, the amniotic egg needs to be laid in subaerial emplacements, either above the ground or into a porous substrate on the vadose zone. The emergence of sands is thus a condition for successful amniotic egg burial. Therefore the presence of autochthonous fossil dinosaur eggs in these marine rocks indicates that the eggs were laid in freshly emerged sands at the sea shore, before the plants colonize the beach. That is the case for example of Llabusta and Suterranya sites at the northern flank of the Tremp basin, were large dinosaur eggs and clutches preserved inside the marine sandstone bodies are the only emergence signs (figures 9-10).

b) land snails indicate emergence as well. In addition to the eggshells, other eggsites from the Aren Sandstone (such as the yellow sandstones from Moro and Alsina, or the reddened sandstones from Bastus and Compuertas) show the presence of *Lychnus* and other land snails (*Cyclophorus*, Bulimids) as a second emergence signal. These terrestrial snails probably lived on plants at the sea shore, like modern land snails. Freshwater rapidly accumulates on the sandy ground after the retreat of the sea, allowing land plants live on the sand dunes of the beaches close to the sea, and on the abandoned cheniers of the strandplain. In spite of claims by Sander *et al.* (1998), the presence of *Lychnus* in Bastus already signalled by Sanz *et al.* (1995) does not contradict the interpretation of the site as a marine beach. It merely indicates the presence of vegetation on the emerged sand dunes, similarly to recent pulmonate snails very abundant on the plants at the shore.

c) pedogenetic features overprinted to the previous signs of emergence. In some particular eggshell sites, a longer exposure is indicated by rubefaction on top of the eggshell-bearing sandstone bodies, and the presence of red or lemon-coloured iron crusts (figures 11 and 12). Ferruginized fossil wood and plant remains are also observed. Moreover, cutane paleosol features and nodulization can appear (figure 14). These evidences indicates oscillation of the water table in the vadose zone and longer subaerial exposure of the sand. The eggshells of these reddened sandstones are white coloured, which usually indicates the lost of the organic matter.

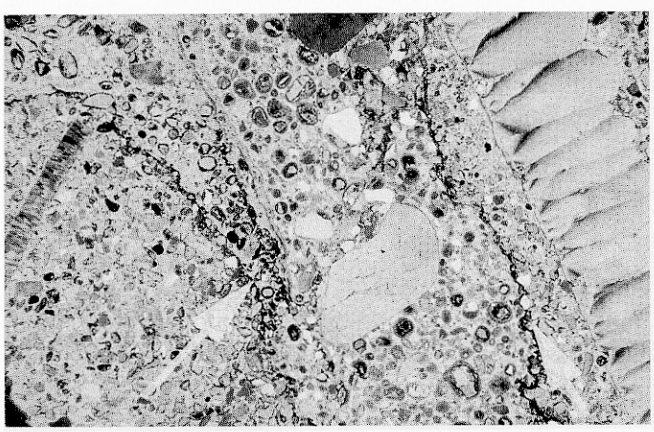


Figure 14. Thin slide of the eggshell-bearing sandstone from Bastus-1. A thin ornithoid eggshell (at the left) and a thick dinosauroid one (at the right) are included in a fine-grained hybrid arenite containing marine bioclasts surrounded by rim haloes; this host-rock is cut by cutane fissures (in the centre of the photograph), filled up by coarse-grained sandstone with abundant, dark pisoids. White arrows indicate the clean boundaries between the pedogenetic features and the clean eggshell-bearing marine host rock, incipiently lithified (see figure 11).

Particularly at Bastus sites, a stronger subaerial exposure and weathering is indicated by the brecciation of the host rock, showing gradual stages which affect it in different degrees. The surface of the sandstones preserves fine- to coarse cracks filled by ironstone. This implies an early lithification of the egg-bearing sandstone (beach-rock type), indicated by incipient rim haloes around the sand components (see figures 11 and 14). Subsequently, this primary eggshell-bearing host-rock was affected by pedogenic processes, signalled by pisoids and cutane pedogenetic features

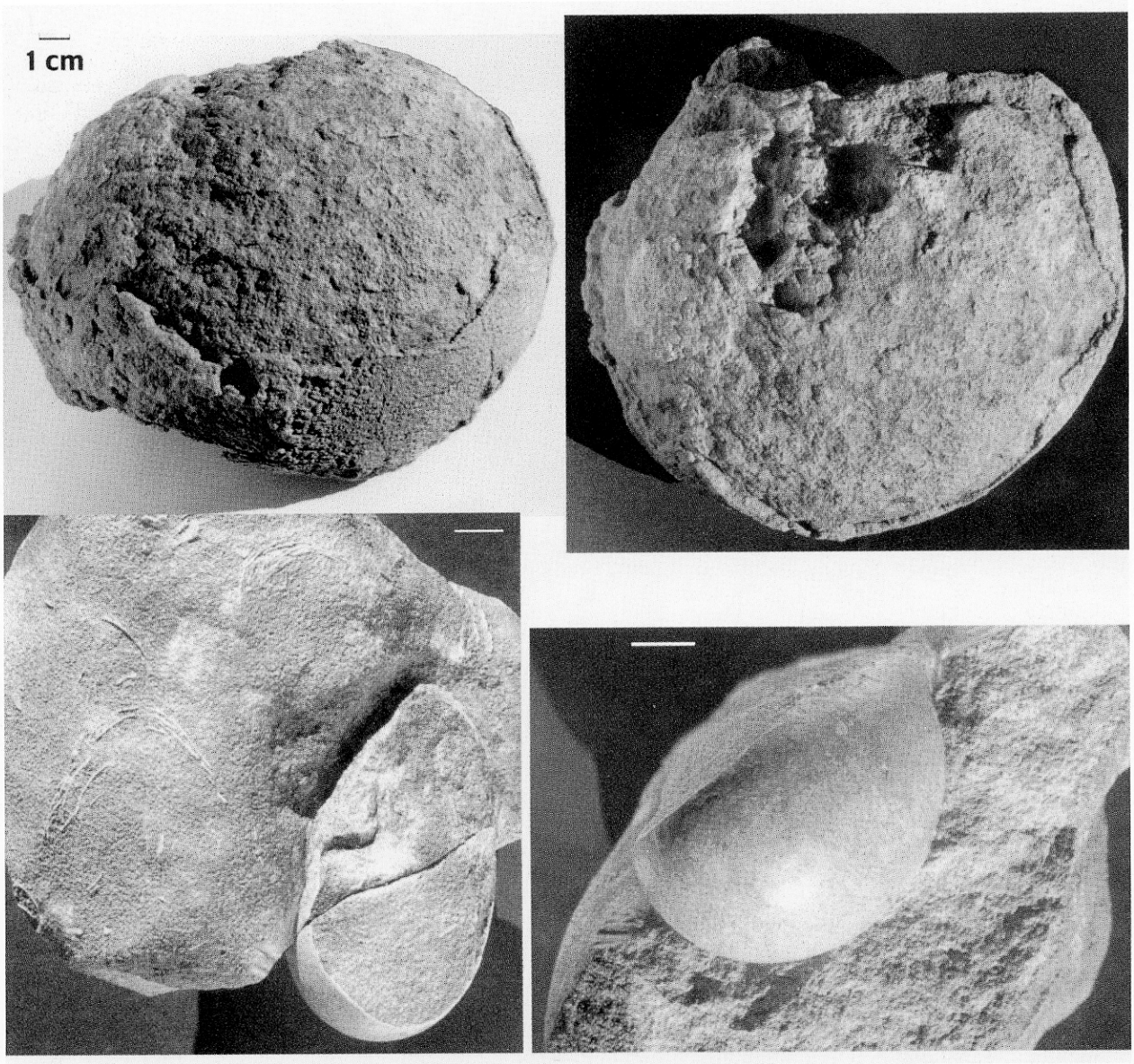


Figure 15. Fossil eggs from the Aren Sandstone, preserved in their original three-dimensional shape. Above, Megaloolithidae near-spherical egg from Suterranya-3. Below, Prismatoolithidae ovoid egg from Cellers-2. Photographs, E. Bernáldez. Housed in the Departamento de Paleontología, UCM.

which cut the original eggshell-bearing sandstones (figure 11). The eggshells were thus already incorporated as a part of the host rock, well before the beccification and the development of the soil. On top of the sandstone, white carbonate nodules and rhizocretions indicate calcimorph paleosol development, reworking the eggshell material buried in the emerged, abandoned beach sands.(Sanz *et al.*, 1995; see figures 11 and 14).

All the observed cases of heavily oxidized, reddish Aren Sandstone eggsites correspond to localities from the Northern flank of the Tremp syncline, e.g. Cal Borrell, Bastus, Vilamitjana, Compuertas and Talarn (figures 2 and 6). Similar reddened surfaces appear regularly westwards in younger Aren Sandstone outcrops, like Sopeira, Orrit and Aren, but eggshells have not yet been found there.

In other rare cases, such as the laterally equivalent sediments eastward of Bastus-2, the eggshell-bearing sandstones show variegated colours (yellow-violet), mottling and bioturbation with hardened tubes filled by *meniscus*. In these cases the eggshells are black-coloured, indicating they have preserved the organic matter in a reducing paleoenvironment, probably stagnant waters at the backshore.

Type of eggs and eggshells

In the Aren Sandstone sites, the preserved eggs generally keep a near original three-dimensional shape (figures 9 and 15), since the sandstone framework is less significantly affected by compression, in con-

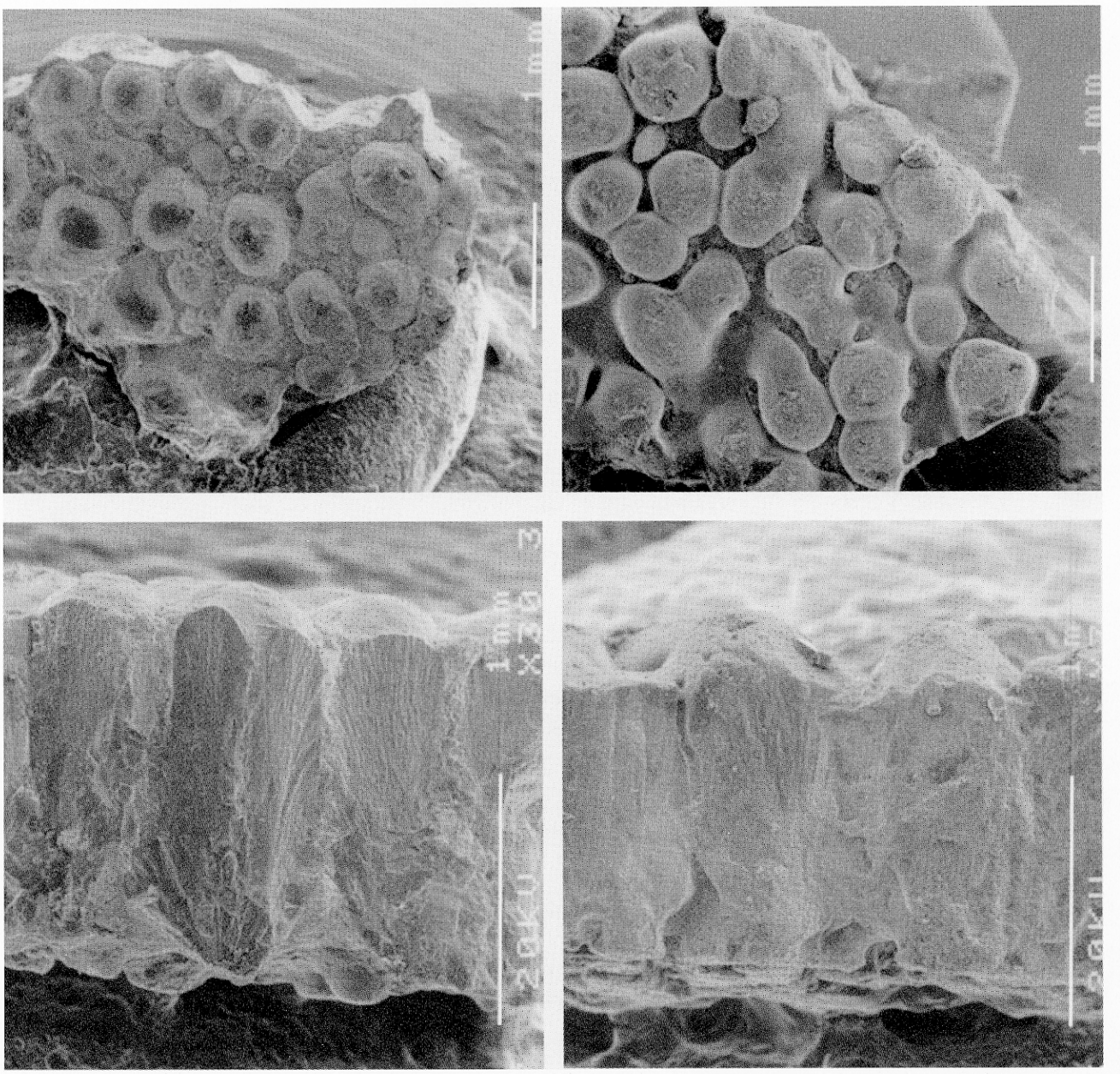


Figure 16. Scanning electron microscope images of tubospherulitic dinosauroid eggshells from Bastus-1 (left) and Suterranya-2 (right). Above, external surface; below, radial section. *Megaloolithus mamillare* from Bastus-1 is thicker and has more independent shell units and nodes; *Megaloolithus pseudomamillare* from Suterranya-2 is thinner and has more confluent shell units and nodes. Scales indicate one millimetre.

trast with the soft marls and clays. Complete eggs are rarely found, because those which are visible have been affected by the recent erosion. Several eggs from Bastus are housed in the Institut für Paläontologie, Berlin (Germany) (Moratalla, 1990).

Typically the *cascarenites* of the Aren Sandstones type-1 eggsites contain low-diversity eggshell assemblages with one to three eggshell types. In all observed cases, the largest eggshell belongs to the dinosauroid tubospherulitic type (oofamily Megaloolithidae), about 2 mm thick, having an ornamented external surface sculptured with rounded, hemispherical nodes (figures 15 and 16). Different oospecies can be distinguished in these eggshells according to their microstructural features, e.g. *Megaloolithus aureliensis* in Moro, M. *mamillare* in Bastus and M. *pseudomamillare* in Suterranya (Vianey-Liaud & López-Martínez, 1997, figs. 8, 14 and 16). This oofamily has been attributed to titanosaur sauropods, according to their coincident geographic distribution (India, South America, Southern Europe) and its association with embryos (Chiappe *et al.*, 1998). Bones of large titanosaur sauropod have been found in the Late Cretaceous of the Pyrenees, attributed to the genus *Hypselosaurus* (Lapparent & Aguirre, 1956; Casanovas *et al.*, 1987).

Other eggshells types present in the Aren Sandstone assemblages are thinner and have smooth exter-

nal surfaces (figure 15). They belong to the prismatic eggshell type (oofamily Prismatolithidae), either ornitoid or dinosauroid type, which have been attributed to theropod dinosaurs and birds by its associated embryos and brooding adults (Varricchio *et al.*, 1997). Other dinosaur families present in the South-central Pyrenees have other eggshell types: e.g. hadrosaurs have prolatospherulithic eggshells; ankylosaurs have not been associated to any eggshell type by now.

Some eggsites from the Aren Sandstone also contain fossil bones together with the eggs and eggshells. The Bastus-1 site preserves the richest bone assemblage, yielding fragments of teeth (mainly crocodiles), large and small scattered bones (large dinosaur long bones, small bone fragments, dermal plates, etc.), patches of smashed tiny bones (probably young dinosaurs) and articulated parts of skeletons, such as an archosaur feet and even an associated skull, backbone and leg bones of a small lizard, likely an egg-predator. However, in spite of the high number of observed cases, bones have not yet been found inside the eggs. Many of the observed eggs show signs of having been hatched; for instance, they keep about half surface, and also preserve fallen fragments inside; also some observed shells show craters in the internal surface, produced by reabsortion of mineral during the last stage of development of the embryos.

EGGSITES IN THE TREMP FORMATION

The Tremp Formation has provided sixteen egg-bearing fossil localities (Table I) with more than eighty fossiliferous levels. The type 1 eggsite is absent, but type 2 is rather frequent, i.e. a recurrent nesting area with many superposed egg-bearing beds in a single section (Coll de Nargó, Graells, Sta. Eulària, Sellent, Faidella and Abella).

The lithologies containing eggs are diverse, e.g. limestones, grey marls, bioturbated siltstones, variegated claystones, fluvial sandstones, coarse conglomerates, etc. Consequently, the nesting depositional environments were also diverse, and also the eggshell types represented in these assemblages. Like in the Aren Sandstone sites, thick Megaloolithidae eggshells are far the most frequent type found in the Tremp Formation.

Periaquatic nests from La Posa Grey Marls

In the Tremp syncline, the lower member of the Tremp Formation is 130 m thick and consists of grey marls with minor intercalations of coal-bearing limestones and coquina beds made by corals and rudists and other mollusc shells (La Posa Grey Marls). This member is equivalent to Unit 1 in the Ager syncline, which consist mainly in peritidal limestones rich in *Girvanella* algae, foraminifera and charophytes, with minor intercalations of grey marls. These deposits have been interpreted as formed by a lagoon-barrier island system, where the Aren Sandstone represents the barrier island and the lower member of the Tremp Formation, with mixed marine-freshwater fauna, represents the lagoon and tidal flats (figure 17; Nagtegaal, 1983; López-Martínez *et al.*, 2000).

Dinosaur bones and footprints have often been reported from this member, but only occasionally eggshells (Bco. de la Munya, Rosell 1967). An exceptional finding in La Posa Grey Marls is a rather complete clutch with seven eggs dated in latest Campanian from Biscarri (near Llordá, housed in the Museo Municipal of Isona; López-Martínez *et al.*, 2000). The preserved lower half of the clutch was included in soft, pyrite-rich grey marls and penetrated by limonitic root casts (figure 18). The slightly elongated eggs, preserved in near vertical position, were not hatched. The fossil content of the surrounding sediment consists in plant debris, euryhaline molluscs, crustaceans, rays and an ankylosaur tooth. The wet mud is an unsuitable substratum for nest burial, because it impedes air conductance. Therefore this nest setting is not compatible with burial of the nests, but instead with nesting on the surface of the substratum, in contrast with the burial pattern shown by the clutches from the Aren Sandstone and other sites (Erben *et al.*, 1979; Sanz *et al.*, 1995). This autochthonous clutch documents a dinosaur nesting habitat in tidal flats above a waterlogged soil, not found in terrestrial species; thus the Biscarri clutch constitutes a palaeobiological evidence indicating a periaquatic habitat for these dinosaurs.

The eggshell type of the Biscarri clutch belongs to the oospecies *Megaloolithus siruguei*, one of the thickest tubospherulitic dinosauroid oospecies characterized by a braided network of pore canals thus enhancing the permeability of the eggs (figure 19; Elez *et al.*, 1999; Moratalla *et al.*, 1999). This feature seems to be linked with the humid paleoenvironment and the mound-nesting pattern, which suggest a nesting behaviour for the Biscarri dinosaur similar to what is known from crocodiles, alligators and some periaquatic birds, that nest on plant-mounds above waterlogged soils, or even on floating vegetation. (López-Martínez

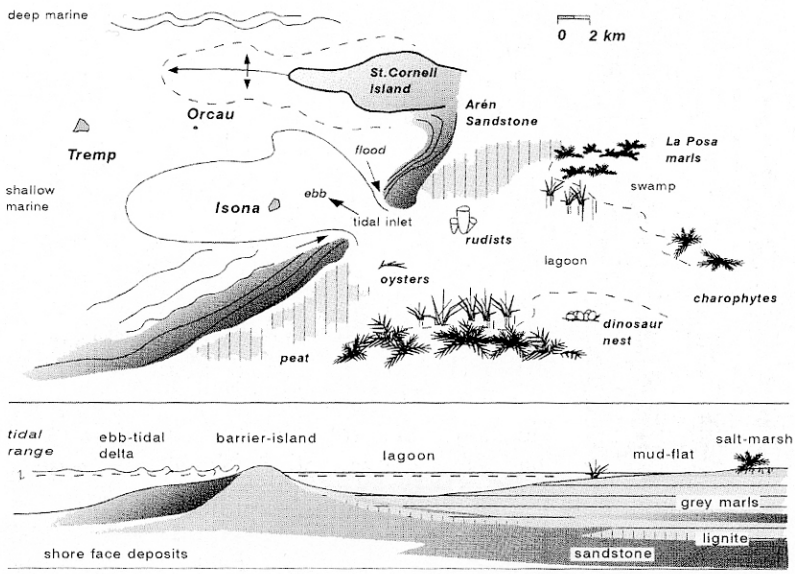


Figure 17. Reconstruction of the paleoenvironment at Biscarri eggsite near Llordá, Isona (Lleida), showing the relations between Aren Sandstone (barrier-island and ebb-tidal delta) and La Posa Grey Marls, lower member of the Tremp Formation (lagoon and tidal flats). From López-Martínez *et al.* (2000, Figure 2), based on Nagtegaal *et al.* (1983).

et al., 2000).

Other examples in the Abella and Coll de Nargó localities show also dinosaur clutches included in grey marls and peritidal limestones from the Unit 1 of the Lower Tremp Formation. Most of these eggshells are close to the oospecies *Megaloolithus siruguei* (figures 8 and 19), but there are also other Megaloolithidae oospecies with thinner eggshells. Apparently complete, undisturbed dinosaur clutches are found in these tidal flat deposits, originally waterlogged sediments. A simple depression or a mound-nest structure may be inferred for these clutches deposited in a reducing dump mud. Up to seven eggs have been observed, although two to five eggs are more commonly found. Some of these clutches are housed in the Museo de Paleontologia de Sabadell (Barcelona).

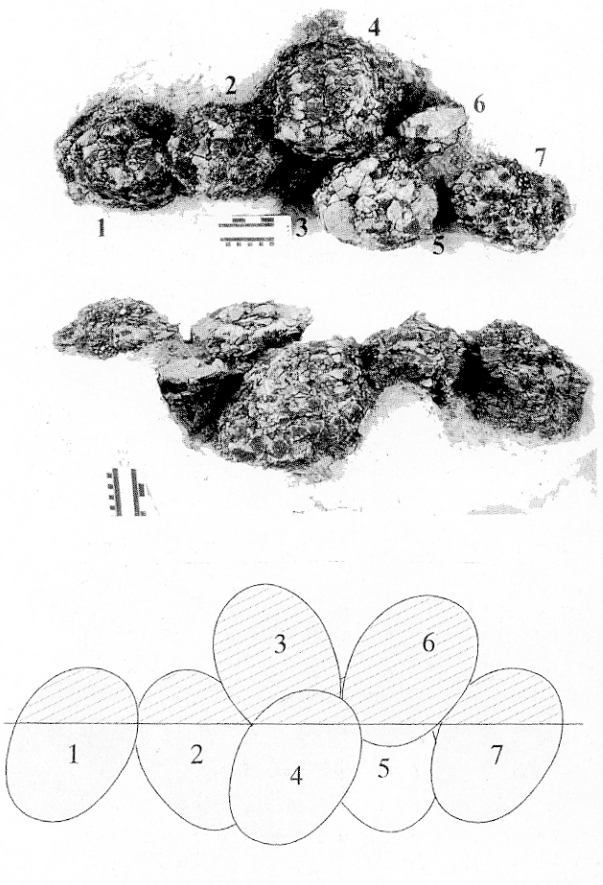


Figure 18. Dinosaur clutch with seven eggs from La Posa Grey Marls (Late Campanian) at Biscarri (near Llordá), in apical and lateral view. The sketches below represents the reconstruction of the original position of the eggs, the preserved part represented in white colour and the missing parts with oblique strips. Housed in the Museo Municipal at Isona (Lleida). From López-Martínez *et al.* (2000, Figure 3).

Bioturbated siltstones, sandstones and conglomerates.

The lower part of the Tremp Formation often presents bioturbated siltstones and variegated claystones, sometimes interrupted by calcimorph paleosols features (root cast, carbonate nodules). Intense bioturbation con-

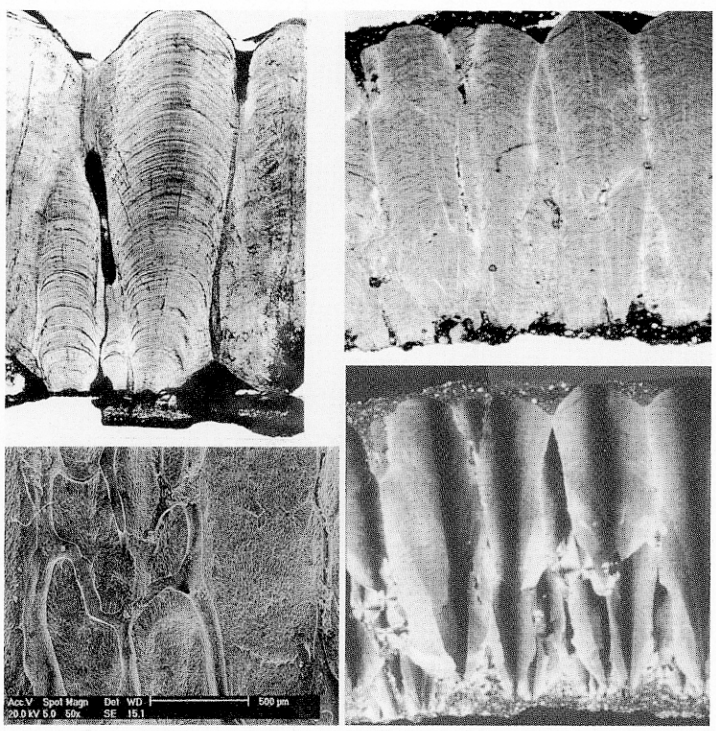


Figure 19. Microscope views of two eggshell sections from the thick dinosauroid tubospherulitic oospecies *Megaloolithus siruguei* (Vianey-Liaud *et al.*, 1994) from Biscarri (left) and Sellent (right). Thin slide from Biscarri above with high, well differentiated shell units and growth lines (optic microscope, parallel nichols) and surface section below showing the network of pore canals (scanning electron microscope) (From López-Martínez *et al.*, 2000, figure 4).Thin slides from Sellent in optic view with parallel (above) and crossed nichols (below) showing a high number of secondary nuclei. Thickness of the radial sections, about 3 mm. photographs, O. Kälin (thin slides) and J.J. Moratalla (SEM).

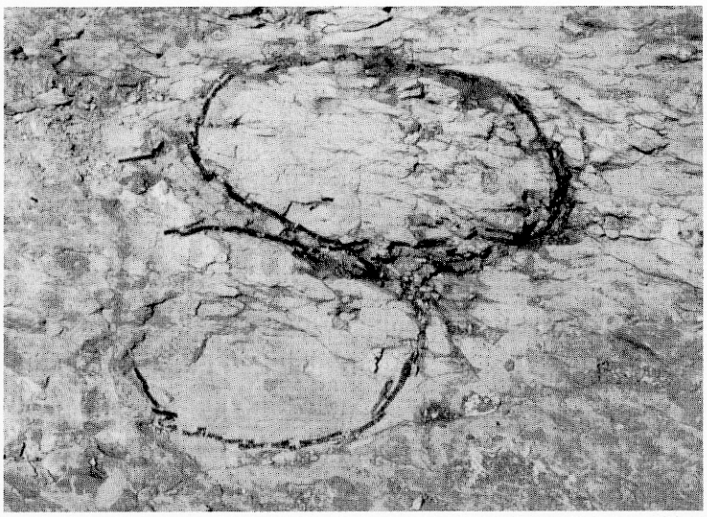


Figure 20. A clutch with two associated eggs (a third egg is badly preserved far at the right) in bioturbated, mottled siltstones at Faidella (East of Abella, Isona area, Lleida), a recurrent nesting area from the Uppermost Campanian of the Tremp Formation.
Figure 21. Fragments of thick eggshells, Late Paleocene in age, from the upper part of the Tremp Formation at Claret (near Tremp, Lleida). Left, macroscopic views of different eggshell types (1,5 magnifications). Three of them show the inner surface (above), the first one with conspicuous reabsortion craters (indicating a hatched egg). Right, microscopic view of a radial thin section of the first eggshell type, coincident with the ratite Elongathoolithidae oofamily, with crossed (above) and parallel nichols (below). Photographs by E. Martin and O. Kälin.

sists in *Ophiomorpha*-like burrows and striotubules showing *meniscus* bands in section, probably produced by crustaceans. Orange, reddish, brown and violet colours are observed, with occasional layers or lenses of grey marls, and thin, discontinuous nodular limestone beds. Mangrove-like swamps have been suggested as the probable environment producing these sediments (Díaz Molina, 1987). Dinosaur eggs with thick Megaloolithidae eggshell type are frequently observed in the bioturbated siltstones.

This sediment type holds some of the major recurrent nesting areas (type 2 eggsites), such as Coll de Nargó and Faidella (figure 20). These consists in repeatedly superposed egg-bearing beds having undisturbed clutches in a near-regular distribution, roughly like the squares of a chessboard. The clutches contain usually three to five, rarely seven eggs. When two clutches coincide in a single bed, they lie far apart from each other. Isolated clutches (type 3 eggsites) and sparse eggshells (type 5 eggsites) have been seen as well in bioturbated siltstones (e.g. Santa Eulària, Vicari, etc.).

Intercalations of fluvial-estuarine sandstone bodies and local conglomerates are rare and thin at the base of the Tremp Formation, and increase and coarse progressively upwards, when pass to Unit 2. These sediment types usually bears mixed assemblages (type 4 eggsites, e.g. Fontllonga-6) and rarely isolated clutches (type 3 assemblages, e.g. Abella- 2).

Sparse eggshell fragments are often found in conglomerates (type 5 eggsites, e.g. Sellent, Faidella, Sant Romà; see Table I). Complete eggs or clutch have not been found in coarse detritic lithologies. Plaziat (1972) refers complete dinosaur eggs in the conglomerates at Coll de Nargó, proving their Cretaceous age against the Tertiary age attributed to them by Garrido Megías & Ríos Aragües (1972); these conglomerates are related to the growth of the Boixols anticline. The dinosaur eggs are in fact preserved in bioturbated siltstones intercalated in conglomeratic beds at Sellent, 8 km west from Coll de Nargó, and correspond to a unit older than the Coll de Nargó conglomerates.

Megaloolithidae are usually the most common eggshell type in these assemblages. In Fontllonga-6 seven dinosaur and avian groups are represented by ootaxa (see above), while the abundant bones and teeth represent only three groups: a sauropod, a theropod and an ornithopod.

Uppermost Maastrichtian eggshells

Dinosaur remains are found until the very Late Maastrichtian in the South-central Pyrenees (López-Martínez *et al.*, 1998; Canudo *et al.*, 1999). One of these youngest eggsites is a 6,5 m thin grey marl lens named Blasi-2 near Aren (Huesca), located on the lowermost part of the highly diachronous Tremp Formation which becomes younger westwards. It has been correlated with oceanic deposits dated with planktonic foraminifera from the uppermost Cretaceous *Abathomphalus mayaroensis* Biozone (López-Martínez *et al.*, 1999a; *in press*).

Blasi-2 contains large dinosaur bones and teeth together with eggshells and abundant remains from other vertebrates. It presents a mixed assemblage (type 4 eggsite) with at least seven eggshell types. The thickest one is a rather thin (about 0.75 mm) dinosauroid tubospherulitic Megaloolithidae eggshell type with undulating external sculpture instead of nodes or tubercles. In spite of a strong sampling effort, no thick tuberculate Megaloolithidae has been found. Six other much thinner eggshell types correspond to the prismatic basic type, either dinosauroid or ornithoid. At least one of them belongs to the Prismatoolitidae oofamily. The diversity based on eggshells (seven types) is again larger than that based on bones and teeth (five types: a hadrosaur, a sauropod and three theropods).

In the Ager syncline (20 km south of Tremp) the Cretaceous-Tertiary boundary has been situated near the top of the Unit 2 of the Tremp Formation without apparent break in the sedimentation, close to

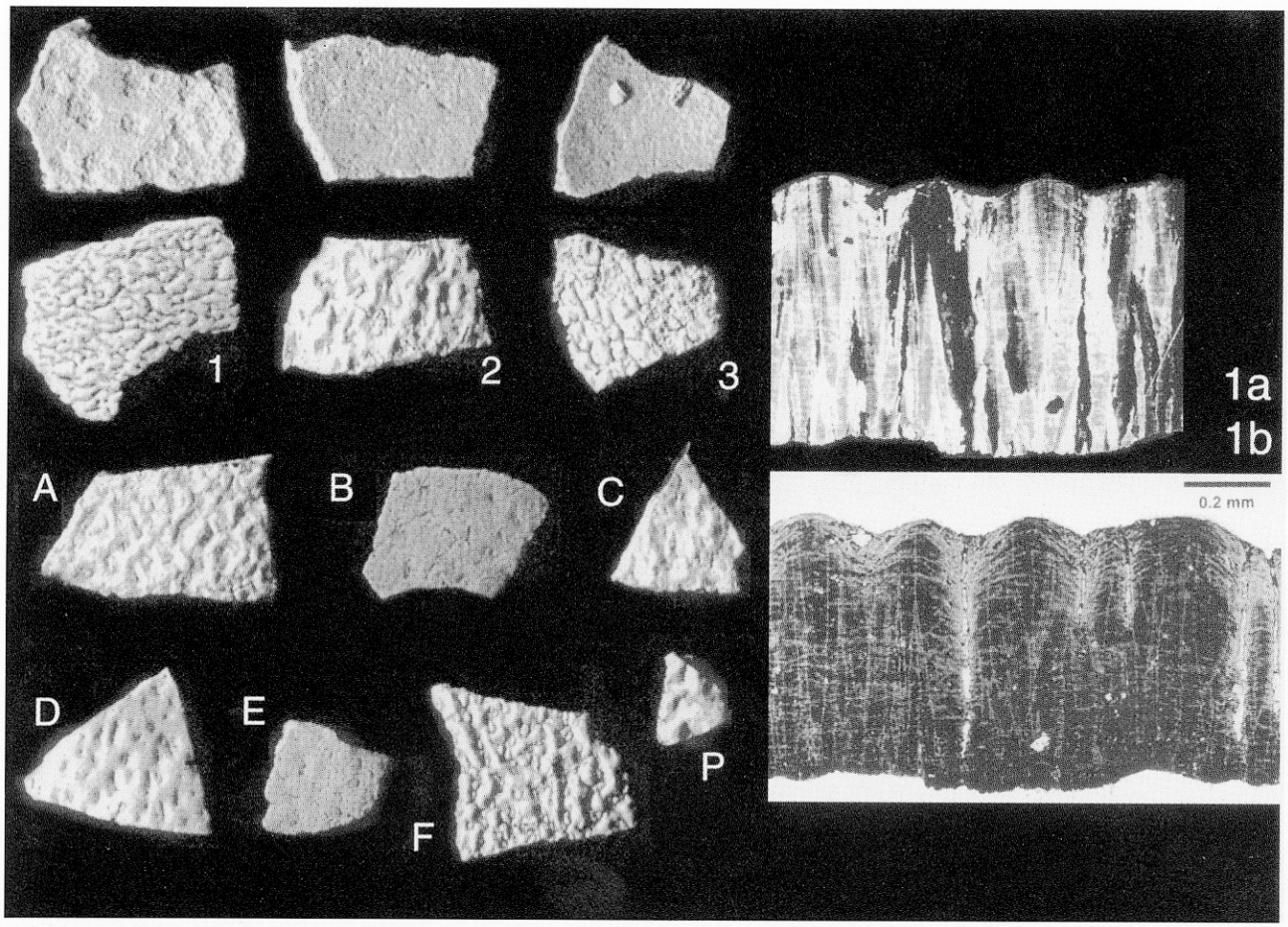


Figure 21. Fragments of thick eggshells, Late Paleocene in age, from the upper part of the Tremp Formation at Claret (near Tremp, Lleida). Left, macroscopic views of different eggshell types (1,5 magnifications). Three of them show the inner surface (above), the first one with conspicuous reabsortion craters (indicating a hatched egg). Right, microscopic view of a radial thin section of the first eggshell type, coincident with the ratite Elongathoolithidae oofamily, with crossed (above) and parallel nichols (below). Photographs by E. Martin and O. Kälin.

the top of a 15 m thick sandstone succession known as the "Reptile Sandstone" (figure 4). This dating is based on biostratigraphy (vertebrates, palynology, charophytes), palaeomagnetism and C^{13} isotopic anomalies. Abundant fish and rare mammal bones and teeth are present in two localities dated in the earliest Paleocene, just three meters above the last Cretaceous level. Development of a large, continuous oncolithic and stromatolithic layer marks these Paleocene upper part of the sandstones (figure 5). Dinosaur bone remains or eggshells have not been found in these assemblages, in spite of a strong sampling effort (López-Martínez *et al.*, 1998).

Paleocene eggshells

Above the "Reptile Sandstone", the sediments of the Tremp Formation in the Ager syncline change from detritic to limestones, paleosols and evaporites passing to Unit 3 of the Tremp Formation, well marked by a rather continuous limestone about 40 m in thickness ("Vallcebre Limestone", figures 4 and 5). Only charophytes and fish have been recovered in the marls intercalated between these limestones, dated in the early Paleocene (Feist & Colombo, 1983).

The youngest eggshell fragments in the Tremp basin are located on the uppermost part of the Tremp Formation (Unit 4), made up by detritic, carbonatic and evaporite deposits intercalated between thick red clays. A rich mixed eggshell assemblage has been recovered by washing and screening several tons of sediments from a grey marl lens below the conglomerates in the Claret village (figure 21). Some scattered eggshells have also been found in grey marls at Tendruy (both localities are situated near Tremp, Lleida, see figure 2). They are associated to mammal, charophyte, *Microcodium* and other fossil remains dated as Late Thanetian (López-Martínez and Peláez-Campomanes, 1999). There are probably autochthonous fossils in this eggshell assemblage, since some of the fragments fit together and correspond to the same egg.

The eggshell fragments are 1 to 3 mm thick and have the surface sculptured with furrows, hollows,

clumps, ridges or folds (figure 21). Some of them are similar to these included in the oogenus *Ornitholithus* from the Late Paleocene of the Aix en-Provenze basin, attributed to giant Carinate birds by Dughi & Sirugue (1959), although there were not associated bones.

At least ten different eggshell oospecies can be distinguished in the Claret assemblage, were no bone remains can be related to the eggshell owners. According to the ongoing study by O. Kälin (figure 21), most of them share a shell structure similar to the ratite Elongatoolithidae oofamily, one of the most widespread ootaxon in the Late Cretaceous of Mongolia and China, associated to Theropoda (Zhao, 1975, 1994; Mikhailov *et al.*, 1994). This eggshell type has also been found in the Late Cretaceous of Northern Pyrenees (Beetschen *et al.*, 1977) and can be related with giant ratite-like fossil bones reported from the Upper Cretaceous of Southern France (Buffetaut *et al.*, 1995), but this type is still lacking in the fossil record of the South-central Pyrenees during this epoch.

DISCUSSION

The rich information from the abundant dinosaur and avian egg fossil record in the South-central Pyrenees sketched in this paper needs detailed studies to extract more conclusive results on nesting behaviour, site-preferences, faunal succession and diversity; here only a brief discussion will follow.

The eggsites from the Aren Sandstone represent the first case in the world of dinosaur eggs recorded in marine facies. The abundance of these eggsites in both flanks of the Tremp syncline indicates a nesting-fidelity behaviour of these dinosaurs. In the northern flank of the Tremp syncline, the Aren Sandstone seems particularly rich in fossil eggs, with a predominance of type-1 eggsites (Cal Borrell, Bastus, Suterranya, etc.). These sites also show a particular alteration of the emerged sandstones, with brecciation, iron crusts and pedogenesis. The proximity to the Boixols growing anticline, which was surely emerged at this moment, may explain the longer emergence time for these beaches and thus a longer dinosaur nesting-site fidelity. These sites were considered as the youngest egg-bearing beds in the biochronology by Vianey-Liaud and López-Martínez (1997), although they appear to be the oldest ones according to recent correlations and dating by planktic foraminifera and rudists (figure 7; Ardèvol *et al.*, 2000; Vicens *et al.*, 1999).

The dinosaur diversity in South-central Pyrenees recognized by means of eggshell types is much larger than that based on bones and teeth. For instance, in Fontllonga-6 seven types of eggshells appear against bones from three type of dinosaurs; in Blasi-2, at least seven types of eggshells against bones from five dinosaur taxa; in Claret, ten types of eggshells against null bone from giant birds. The fossil record of dinosaurs and birds, and thus the data on their diversity and succession, will probably an order of magnitude increase when the fossil eggshells will be fully studied, allowing a better understanding of their evolutionary crisis.

From Late Campanian to Early Maastrichtian, the most abundant eggshell types in the basin are thick Megaloolithidae eggshell types with the external surface sculptured with nodes (figures 8 and 16). They can be attributed to sauropods like other types of Megaloolithidae. Different oospecies of this oofamily occur in Aren and Tremp Formations (sequences Aren-1 to Aren-3, figures 6 and 7; see figures 8, 14, 16, 19). Some Megaloolithidae oospecies are common to both formations (e.g. *Megaloolithus petralta* in Fontllonga-6 and Moro). Others are however extremely frequent in the Tremp Formation but very rare or absent in the Aren Formation (e.g. *Megaloolithus siruguei* in Sellent, Faidella and Biscarri). It can be questioned if this particular oospecies was constrained to these deposits because it was linked to a special environment or to a chronological episode. Both cases are probable, because this oospecies is the most frequent dinosaur eggshell type in Abella and the north-eastern part of the Coll de Nargó syncline, were the Aren Sandstone is thinner; and it is absent in younger eggshell assemblages of the Aren and Tremp Formation (sequence Aren-4, Units 3 and 4) with lithologies and thus sedimentary environments very similar to the previous sequences. Similar oospecies are also present in Northern Pyrenees and Aix en-Provence basin (Vianey-Liaud & López-Martínez, 1997).

The abundance of Megaloolithidae eggshells during the Campanian and Early Maastrichtian in South-central Pyrenees points out to a rich population of sauropod dinosaurs. The sauropods were supposed to be extinct during the Maastrichtian in Europe, although their presence in South-central Pyrenees has been documented until the Late Maastrichtian (Canudo *et al.*, 1999). Nevertheless, a decrease of this group during the Maastrichtian is supported by the rarity of tuberculate Megaloolithidae eggshells in the Aren-4 sequence (Late Maastrichtian). At the northern flank of the Tremp syncline, the reddened western Maastrichtian outcrops of the Aren Sandstone seem completely to lack dinosaur eggs, although they are very similar to that of the rich eastern Campanian outcrops. It is probable that a different group of Late Maastrichtian sauropods with thinner, undulating eggshell surface replaced the Campanian shore-nesting

sauropods with ticker, tuberculate eggshell surface.

Conversely, the diversity of prismatic eggshell types seems to increase during the Maastrichtian, in agreement with the apparent increase of Theropoda at this moment (López-Martínez *et al.*, *in press*). The dinosaur and avian fossil record based on eggshells provides much higher diversity that the one based on bones.

The absence of eggsites during Early Paleocene seems to be significant, since they were very abundant in similar sediments in the area during Cretaceous times. An ecological crisis in the terrestrial environments, marked by the extension of stromatolites and *Microcodium* may be related to this absence.

The eggshell-bearing beds of upper Tremp Formation dated as Late Thanetian (Latest Paleocene) contains a rich assemblage of ratite-like ootaxa which are very similar to the Late Cretaceous Elongatoolithidae Asiatic oofamily, also recorded in Northern Pyrenees, probably belonging to giant birds. It shows the recovery of the egg assemblage richness and diversity in South-central Pyrenees after an hiatus of about nine million years. The intermediate beds of Early and middle Paleocene age have not yet provided fossil eggshells in any part of the world to document the history of these peculiar *Lazarous* ootaxa.

CONCLUSIONS

The South-central Pyrenees deposits have preserved egg and eggshell assemblages from thirty three localities, containing more than one hundred eggsites and thirty eggshell oospecies. Their age ranges from Upper Campanian to Late Thanethian. They are found in sediments from the Aren and Tremp Formations, which are in part laterally equivalents. Four depositional sequences, Aren-1 to 4, have been recognized for the Late Cretaceous Aren Sandstone and Lower Tremp Formation. The eggshell-bearing beds belong mainly to the Aren-2 sequence; the Aren-1, 3 and 4 are much poorer in eggsites.

Five types of eggsites can be distinguished, three of them with autochthonous assemblages (type 1, high occupation site; type 2, recurrent nesting area; type 3, isolated clutch) and two of them with allochthonous assemblages (type 4, mixed assemblage; type 5, sparse eggshells).

The type-1 eggsite is exclusive of the Aren Sandstone sites, which represent the colonisation of abandoned marine beaches by dinosaurs burying their eggs repeatedly, until the sands became rich in eggshell fragments (*cascarenite*). This marine turtle-type of nesting behaviour is unique in the fossil record of dinosaurs.

Several findings of isolated clutches in grey marls and a complete clutch recovered from tidal flats sediments of the Lower Tremp Formation indicate a mound-nesting pattern above the wet mud in a peri-aquatic environment. This alligator-type of nesting behaviour is also unique in the fossil record of dinosaurs.

Other eggsites have been found in bioturbated siltstones, fluvial sandstones and conglomerates from the Tremp Formation. The Megaloolithidae oofamily, attributed to sauropods, is the most common eggshell type in the South-central Pyrenees. Other eggshells belong to prismatic (dinosauroid and ornithoid) and ratite types.

The eggsites become rarer during the Maastrichtian and absent in the Danian. Rich ratite-like eggshell assemblages are documented in Late Thanetian, showing the recovery of the ecosystems. They belong to the Elongatoolithidae oofamily, well-known in the Late Cretaceous of Asia and also present in Northern Pyrenees. They are attributed to giant birds and non-avian Theropoda. Its survival into the Tertiary, after an hiatus of about nine million years, makes it a significant evolutionary *Lazarous* taxa.

ACKNOWLEDGEMENTS

This work contains data recovered during eight years of field studies and discoveries made with L. Ardèvol (Geoplay), M.E. Arribas (UCM), A. Lacasa (IEI), B. Marandat (USTL) and E. Vicens (UAB), with the help of M.A. Álvarez-Sierra, J. Civis, late R. Daams, A. González, S. Krauss, F. Ortega, P. Peláez-Campomanes, A. de la Peña, B. Pérez Moreno, P. Sevilla, B. Sigé, R. Soler Gijón and M.F. Valle during the study, and of F. Albert, A.Baus, S. Díaz, J. Expósito, I. Pérez and J. Pocino during the field work. M. Díaz Molina, O. Kälin, J.L. Moratalla, J.L. Sanz and M. Vianey-Liaud provided their invaluable experience during the different phases of the study and contributed to the interpretation of the Bastus sites. A. Bravo and T. Reyes made the editorial work. Thanks are due to the local institutions and people of the Pyrenees, particularly Ajuntament d'Isona i Conca Dellà, C.I.T.A. Consell Comarcal del Pallars Jussà and Hotel Terradets (Cellers) for their kind support. Funds were provided by the DGES projects PB91-0315, PB95-0398 and PB98-0813 from the Spanish MEC.

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